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Oxygen Consumption Rates and Metabolic Enzyme Activities of Oceanic California Medusae in Relation to Body Size and Habitat Depth

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Abstract. Oxygen consumption rates were measured in 14 species of hydromedusae and 5 species of bathypelagic coronate scyphomedusae. Analysis of all individuals of all species of medusae showed the familiar pattern of decreasing specific oxygen consumption rate with increasing wet weight of animals. Citrate synthase (CS), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and pyruvate kinase (PK) activities were measured in more than 30 species of medusae. Octopine dehydrogenase, strombine dehydrogenase, and alanopine dehydrogenase were not detected in either hydromedusae or scyphomedusae. The allometric scaling phenomenon of decreasing activity in larger individuals was observed in Krebs cycle enzyme activities. LDH activities, on the other hand, increased with increasing wet weight. Most medusae were aerobically poised, with higher CS activities than LDH activities. However, several meso- and bathypelagic medusae, including the coronate scyphozoans *Periphylla periphylla* and *Nausithoë rubra*, were anaerobically poised, possibly as a mechanism to assist in vertical migrations at low oxygen concentrations in the oxygen minimum layer. There is poor correlation between CS activities and oxygen consumption rates in these medusae when compared to previously investigated animals. To account for this poor correlation, we propose the hypothesis that medusan CS at the periphery of the maximum diffusion distance may be oxygen-limited and does not function at the normal *in vivo* rate. For pelagic medusae, there is no apparent decline in metabolic rate and metabolic potential, as determined by enzymatic activity, with increasing depth of occurrence, beyond the declines caused by the decrease in temperature with depth. These patterns are in contrast to the rapid declines in metabolic rates and metabolic potentials with depth that have been observed for pelagic fishes and crustaceans. Deep-living medusae have metabolic rates of a magnitude similar to those of bathypelagic fishes and crustaceans.

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Introduction

Previous studies on the metabolic rates of medusae have been mainly restricted to the more common near-shore species (*e.g.*, Arai, 1986; Larson, 1987b, and references cited therein). The few physiological and biochemical investigations on deep-living gelatinous organisms include measurements of the *in situ* respiration of the bathypelagic scyphomedusa *Poralia rufescens* (Smith, 1982); the metabolic rates of the midwater ctenophore *Bathocyroe fosteri* (Youngbluth *et al.*, 1988); and the oxygen consumption rate of the gelatinous pelagic holothuroid *Scotoanassa* sp. from the benthic boundary layer off southern California (Childress *et al.*, 1989). In addition, we recently measured the respiratory rates and enzyme activities of the gelatinous polychaete *Poecobius meseres* and some other deep-sea worms and chaetognaths (Thuesen and Childress, 1993a, b).

One method of estimating aerobic metabolic rates from enzymatic activities involves measurement of the activity of the electron transport system (ETS) (Båmstedt, 1980; Mayzaud, 1986; Packard, 1979; Packard *et al.*, 1975; Packard *et al.*, 1988). This method has been applied to various types of zooplankton, including three species of epipelagic hydromedusae by King and Packard (1975). They observed lower metabolic potentials (ETS activities) in relation to oxygen consumption for medusae than for other zooplankton. There are no previous studies on the metabolic enzyme activities of medusae.

Many investigators have observed large declines in the metabolic rates of pelagic fishes and crustaceans with increasing habitat depth (Childress and Thuesen, 1992). The oxygen consumption and nitrogen excretion rates of pelagic crustaceans and the metabolic rates and metabolic potentials, as estimated by enzyme activities, of pelagic fishes, decline rapidly with increasing depth of occurrence (Childress, 1971, 1975; Childress and Somero, 1979; Cowles *et al.*, 1991; Ikeda, 1988; Quetin *et al.*, 1980; Sullivan and Somero, 1980; Torres *et al.*, 1979; Torres and Somero, 1988). Protein contents of pelagic crustaceans and fishes also decline as a function of depth of occurrence, but to a much lesser extent than metabolic rates and enzymatic activities (Bailey and Robison, 1986; Childress and Nygaard, 1973, 1974; Childress *et al.*, 1990b; Stickney and Torres, 1989). Differences in temperature, pressure, chemical composition, or size have been estimated to account for only a small fraction of the declines in metabolic rates of these organisms. The corresponding proportional decline of enzyme activities in fish white muscle indicates that the decline in metabolic rate is laid down at the subcellular level (Childress and Somero, 1979; Siebenaller and Yancey, 1984; Somero and Childress, 1980; Sullivan and Somero, 1980; Torres and Somero, 1988).

The visual interactions hypothesis has been proposed to account for the widely observed metabolic declines with habitat depths in pelagic crustaceans and fishes. It suggests that animals that use visual interactions in predator-prey relationships have high metabolic rates to maintain the robust bodies needed to react rapidly over the appreciable distances in which visual interactions take place in high light environments; whereas animals that live in environments where visual interactions are much more limited in distance due to low light levels, or that do not have image-forming eyes, have experienced reduced selection for locomotory capabilities and hence have lower metabolic rates compared to their visual counterparts (Childress and Mickel, 1985; Childress *et al.*, 1980; Childress *et al.*, 1990a). One test of the visual interactions hypothesis is to examine the metabolic characteristics of nonvisual pelagic animals with regard to increasing habitat depth. The visual interactions hypothesis suggests that bathypelagic nonvisual organisms would have metabolic rates similar to their epipelagic counterparts. We have tested this hypothesis by examining the metabolic rates and enzyme activities of California chaetognaths in relation to depths of occurrence, and our observations support the predictions of the visual interactions hypothesis (Thuesen and Childress, 1993a). Meso- and bathypelagic chaetognaths have oxygen consumption rates and enzyme activities comparable to epipelagic species when measured at the same temperature.

Herein we examine the predictions of the visual interactions hypothesis when applied to pelagic medusae—another group of pelagic organisms that do not have image-forming eyes. Gelatinous organisms are important components of pelagic ecosystems, and yet they have historically been overlooked or underestimated in studies on marine ecosystems. In the last decade, the quantitative importance of medusae, ctenophores, salps, and other gelatinous animals in the flow of energy through pelagic ecosystems has been recognized (Alldredge, 1984; Longhurst, 1985). This study is a broad comparison of the metabolic rates and potentials of oceanic hydromedusae and scyphomedusae living at depths down to 2 km. We examined enzyme activities and metabolic rates in relation to wet weight to determine the influence of body size on these parameters; we also looked at the metabolic poise of the medusae in this study by comparing anaerobic and aerobic metabolic potentials.

Materials and Methods

Collection of medusae

Our primary collecting gear was an opening-closing Mother Tucker trawl with a 10-m^2 mouth fitted with a closing 30-l insulated cod end (Childress *et al.*, 1978). The cod end prevented heat shock to animals living below the thermocline and injury due to turbulence while the net was being brought to the surface. Epipelagic medusae were occasionally captured by 200-m wire-out oblique tows of a 1-m ring net. Collections were carried out on the RV *Point Sur* in the San Clemente Basin during September 1988 and in an area about 160 km west of Point Conception, California (123°E, 34°50′ N) in July 1991, and on cruises of the RV *New Horizon* off Point Conception in June 1990 and February and June 1991. The ship speed was kept very low (0.5–1 kn) to decrease turbulence and abrasion in the net and reduce the number of animals collected in the cod end, thereby maximizing the condition of the gelatinous organisms. Animals were transferred to 5°C seawater upon recovery, quickly identified to species, and either held for measurements of metabolic rate or frozen in liquid nitrogen for later analyses of enzyme activity in the laboratory. Every effort was made to select animals with empty manubria and to remove commensal or epizoic organisms.

In addition to these collections, some animals were obtained with the sampling pumps and collecting devices of the Monterey Bay Aquarium Research Institute's ROV *Ventana* in Monterey Canyon in August 1990. Neritic, demersal, and epiphytic medusae were occasionally hand-collected in the Santa Barbara Channel by scuba divers over the course of this study.

The demersal hydrozoan *Polyorchis penicillatus* and the epipelagic hydrozoan *Leukartiara octona* were maintained in a planktonkreisel with an abundant supply of crustaceans, primarily *Holmesimysis costata*, as food for

up to 48 h after capture. They were then held without food for 24 h until their manubria were empty, before being frozen for enzyme activity investigations. Selected individuals of *L. octona* were acclimated to a colder temperature, 5°C, in a planktonkreisel for 1 week under the same food conditions and then used for respiration experiments.

Some specimens that were originally frozen in liquid nitrogen were stored up to 6 months in a −80°C freezer without detectable loss of enzyme activities. Animals collected by meter net and remotely operated vehicle, without thermal protection, were used only for enzyme assay investigations.

The report on the hydromedusae of the Indian and Pacific Oceans by Kramp (1968), Russell's treatises on Atlantic medusae (Russell, 1953, 1970) and the numerous references cited therein were indispensable in our identification of medusae to species.

Metabolic rate measurement

Oxygen consumption measurements on animals that were recovered in excellent condition were carried out either on board ship or in the laboratory. Our previous experiments on the effect of hydrostatic pressure on two bathypelagic hydromedusae, *Crossota rufobrunnea* and *Aegina citrea,* showed no significant differences in metabolic rates measured at 1 and 101 atm (Childress and Thuesen, 1993). Therefore, all metabolic rates were measured at atmospheric pressure. Oxygen consumption rates were measured in two ways, depending on the size of the animal. Larger animals were transferred to water-jacketed respiration chambers of appropriate size containing 5°C filtered seawater with antibiotics (0.20-μm membrane filter; 25 mg l^{-1} each of streptomycin and penicillin) and equipped with small stirring pumps consisting of a magnetic stirring bar enclosed within a discrete plastic chamber. This mechanism allowed for gentle mixing of water and provided sufficient flow for the Clarke-type oxygen electrodes (Mickel *et al.,* 1983) without damage to the animal. Smaller animals were transferred to glass syringes used as miniature respiration chambers (Thuesen and Childress, 1993a). The syringes with filled with filtered seawater containing antibiotics as above and incubated at 5°C. Periodically, a gas-tight syringe was used to withdraw water samples from the incubation syringe through a three-way valve, and the new incubation volume was noted. Before the sample was withdrawn, syringes were turned end-over-end several times to mix the incubation medium. Oxygen and carbon dioxide content of the water was measured with a gas chromatograph (Childress *et al.,* 1984).

Oxygen consumption rates of hydromedusae from the Santa Barbara Channel, *Vallentinia adherens, Eirene mollis,* and *Leukartiara octona,* were measured at 15°C following the latter method. The oxygen consumption rates of acclimated *L. octona* were measured at 5°C. Oxygen consumption rates at 10°C of *Periphylla periphylla* and *Colobenema sericeum* were measured with oxygen electrodes.

Control syringes of filtered seawater containing the antibiotic mixture but without animals were run simultaneously. After removal of the animals, syringe and respirometer experiments were periodically left to continue as controls to check for bacterial contamination. If present, background respiration was subtracted from animal respiration. Background respiration was always undetectable at 5°C. After experiments at sea, animals were weighed using a shipboard motion-compensated precision balance system (Childress and Mickel, 1980). In the laboratory, animals were weighed on an analytical balance. All specimens used in oxygen consumption experiments were later frozen in liquid nitrogen for spectrophotometric analysis of enzyme activities.

Biochemical analysis

The following enzymes were screened to select appropriate indicators of aerobic and anaerobic metabolic potential: citrate synthase (CS, E.C. 4.1.3.7), malate dehydrogenase (MDH, E.C. 1.1.1.37), lactate dehydrogenase (LDH, E.C. 1.1.1.27), pyruvate kinase (PK, E.C. 2.7.1.40), octopine dehydrogenase (E.C. 1.5.1.11), alanopine dehydrogenase (E.C. 1.5.1.17), and strombine dehydrogenase (E.C. 1.5.1.?). Although we assayed for these enzymes in a variety of medusae, our study focused on CS and LDH as two enzymes representative of metabolic potential. CS is an important regulatory enzyme and functions in the first step of the citric acid cycle. MDH plays a variety of roles in intermediary metabolism and is important in the citric acid cycle. These enzymes serve as indicators of aerobic metabolic potential. LDH is the terminal enzyme in glycolysis, and PK is the regulatory enzyme that supplies pyruvate for LDH in the second-to-last step in glycolysis. These two enzymes are excellent indicators of glycolytic potential and contribute to both aerobic and anaerobic metabolic pathways. Because we did not assay the various opine dehydrogenase in all the species in this study, it could be that one or more of these enzymes are better indicators than LDH of anaerobic potential in some species. CS, MDH, LDH, and PK activities in fish muscle have all been found to correlate well with oxygen consumption rates (Childress and Somero, 1979; Somero and Childress, 1990; Sullivan and Somero, 1980; Torres and Somero, 1988).

Whole animals were weighed on a Mettler analytical balance while they were still frozen and were homogenized at a very low dilution (from 1:1 to 1:9 parts weight/volume

in 0.01 *M* Tris homogenization buffer, pH 7.5, at 10°C) in Duall hand-held glass homogenizers kept on ice. Low dilutions were used to detect the low enzyme activities present in medusan homogenates. Very large animals were subsampled by removing a wedge-shaped piece of the whole animal for homogenization. Aliquots of homogenate were transferred to microfuge tubes and centrifuged at 6600 × *g* for 5 min at 5°C. Unlike the enzyme activities of fish muscle, activities in whole-animal homogenates decreased by 20–40% after 4 h standing on ice. Therefore, all assays were performed within 1 h of homogenization, using a Shimadzu UV160U spectrophotometer equipped with a water-jacketed cuvette holder. The subumbrellar, or swimming, muscle of some of the larger species of medusae was readily excised. For these species, the enzyme activities in these muscles were also measured. Small amounts of sample supernatant (10, 25, or 50 μl) were used for assays. To estimate maximum metabolic potential, measurements of enzyme activity were made in 1-ml quartz cuvettes at 20°C under nonlimiting conditions and followed procedures essentially the same as those described previously (Childress and Somero, 1979; Somero and Childress, 1980). Enzyme activities are expressed as units (micromoles substrate converted to product per min) per gram wet weight of animal.

CS activity was measured in a medium containing 50 m*M* imidazole/HCl buffer (pH 7.8 at 20°C), 0.5 m*M* oxaloacetate, 0.1 m*M* acetyl-CoA, 0.1 m*M* 5,5-dithiobis (2-nitrobenzoic acid) (DTNB), and 1.5 m*M* $MgCl_2$. The increase in absorbance at 412 nm due to the reaction of the reduced coenzyme A generated by the enzymatic reaction with DTNB was recorded. Background activity before the addition of homogenate supernatant was recorded, and this background rate was then subtracted from the overall rate after the assay reaction was initiated by addition of the oxaloacetate. Background activity was subtracted from total activity to calculate the enzyme activity of the sample. MDH activity measurements were performed in a medium containing 100 m*M* Tris/HCl buffer (pH 8.1 at 20°C), 20 m*M* $MgCl_2$, 0.4 m*M* oxaloacetate, and 150 μ*M* NADH. LDH activity was measured in a medium containing 80 m*M* Tris/HCl buffer (pH 7.2 at 20°C), 2 m*M* sodium pyruvate, 150 μ*M* NADH, and 100 m*M* KCl. PK activity was measured in a medium containing 50 m*M* imidazole/HCl buffer (pH 7.8 at 20°C), 100 m*M* KCl, 10 m*M* $MgSO_4$, 0.1 m*M* fructose-bisphosphate, 1.0 m*M* phosphoenolpyruvate, 5.0 m*M* ADP, 150 μ*M* NADH and excess LDH activity (rabbit muscle LDH, Sigma Chemical Co.). The assay reactions of MDH, LDH, and PK were started by addition of the sample supernatant, and the decrease in absorbance at 340 nm due to NADH oxidation was recorded.

Lactate concentration in tentacle and swimming muscle tissue of *Periphylla periphylla* and *Aegina citrea* was measured at sea. Frozen tissue was homogenized in 0.1 *M* perchloric acid, neutralized to a pH of 10 with KOH, and centrifuged at 6600 × *g* for 10 min. Lactate concentrations in the supernatant were measured enzymatically using L-lactic acid assay reagents (Boehringer-Mannheim).

Statistical analysis

All statistical analyses were performed with Statview II or SuperANOVA (Abacus Concepts, Inc., Berkeley, CA). Simple linear regressions, multiple regressions, Kendall nonparametric rank correlations, and analysis of covariance (ANCOVA) were used to explore the relationships among the parameters that were measured in this study. Simple linear regressions were used to describe the relationships between various variables, including relationships between weight-specific citrate synthase activity and weight-specific metabolic rates. Regressions of total (not standardized by weight) CS activities *versus* total oxygen consumption rates were not used. Although this statistical methodology has been used in previous studies on zooplankton physiology, it essentially regresses body mass on the *y*-axis with body mass on the *x*-axis, and it thereby results in higher values of correlation coefficients and apparent statistical significance when compared with a slope of zero. It does not, however, test the relationship between enzyme activity and oxygen consumption rate independent of body size. All rates of oxygen consumption and enzyme activity referred to in this study are weight-specific. All the regressions in this study were carried out on ln-transformed data to improve linearity.

Oxygen consumption rates and enzyme activities of medusae were evaluated in relation to wet mass of the animals, and scaling coefficients from the allometric equation $y = aM^b$ were derived, where M is the wet weight of the animal, b is the scaling coefficient, and a is a constant for the species at a given temperature (Schmidt-Nielsen, 1983). Mean values of specific oxygen consumption rates and the enzyme activities of whole-animal homogenates for each species were used in comparisons with crustacean and fish data from the same region (metabolic rate data on pelagic crustaceans [Childress, 1975] and enzyme activities of fishes [Childress and Somero, 1979; Wells and Childress, unpublished]) using ANCOVA to test whether the slopes of the various relationships between minimum depth of occurrence (MDO) and enzyme activity were significantly different. The Kendall rank correlation was used to test for significant relationships between MDO and the biochemical-physiological parameters without any assumptions of form or linearity of the relationships and to find correlations between the biochemical and physiological data. Since these tests are performed on data from within a single region that has a consistent relationship between temperature and depth,

no correction for temperature difference is necessary. MDO in a given region is defined as that depth below which 90% of the population usually can be found (Childress, 1975). A depth of 10 m was taken as the MDO for animals living at 10 m or shallower to avoid distortions in regressions of ln-transformed data. Medusan MDOs are based on our personal observations using the opening-closing Mother Tucker trawl and published bathymetric distributions of medusae off southern California (Alvariño, 1967). When we did not have sufficient data to evaluate MDO for a given species, the shallowest capture depth was used. This was only done for the rarer species of medusae, which were uncommonly captured in trawls. Minimum capture depths for *Tiaranna rotunda*, *Euphysora gigantea*, and *Neoturris fontata* are 650, 350, and 650 m, respectively. The epiphytic medusa *V. adherens* was excluded from depth comparisons of pelagic species.

Wet mass was used as the size measurement, because this parameter is the physiologically significant one that determines constraints on animal locomotion, behavior, etc. Other measurements, such as dry weight or protein content, used as indicators of size can lead to misinterpretations concerning the biology and ecology of the whole organism. The significance of using various parameters of body size in this regard has been discussed previously (Childress, 1977; Childress and Somero, 1979).

Results

Oxygen consumption measurement

Many species of medusae were collected in excellent condition by using the large insulated cod end. These included four undescribed species of Trachymedusae: *Pantachogon* sp. A (*cf. P. haekeli*), *Vampyrocrossota childressi* (Thuesen, 1993), *Tetrorchis* sp. A (distinct from *T. erythrogaster*), and an orange and pink rhopalonematid, *Crossota* sp. A. Very large and fragile animals, such as *Solmissus incisa*, could not be collected in sufficiently healthy condition for oxygen consumption rate measurements; however, smaller fragile animals, such as species of the Halicreatidae, were often collected with tentacles more than several body-heights in length and with intact swimming bells. These animals were still swimming after 24 h in the incubation syringes. Coronate medusae, rhopalonematids, and other robust animals were caught in pristine condition and could be maintained alive and swimming for several days in 20-l buckets in a 5°C refrigerator. Oxygen consumption rates were measured on 14 hydrozoans and 5 species of coronate scyphozoan medusae: mean rates are presented in Table I. Oxygen consumption rates of three species of medusae were measured at two temperatures, and the Q_{10} for *Leukartiara octona* and the estimated Q_{10} values for *Colobenema sericeum* and *Periphylla periphylla* are 3.5, 4.8, and 2.6, respectively.

Analysis of all individuals of all species of medusae showed the familiar pattern of decreasing oxygen consumption rate with increasing wet weight of animals at both 5° and 15°C (Fig. 1). Scyphozoans analyzed as a separate group also showed a highly significant relationship between size and metabolic rate ($b = -0.26$; F test for regression coefficient, $P < 0.01$, 95% CI: ±0.17). However, among the hydrozoan medusae there was a less significant effect of size on metabolic rate ($b = -0.13$; F test for regression coefficient, $P = 0.07$, 90% CI: ±0.11). Although analysis of most species over a large enough size range with a sufficient number of individuals to determine species-specific scaling patterns was not possible, it was undertaken for *Aegina citrea*, *Crossota rufobrunnea*, and *Periphylla periphylla*. A significant size-metabolism relationship was found only for *C. rufobrunnea*, which had a scaling coefficient of −0.31 (F test for regression coefficient, $P = 0.02$; 95% CI: ±0.25).

Enzyme activity

Citrate synthase, lactate dehydrogenase, pyruvate kinase, or malate dehydrogenase activities were measured on more than 150 individuals of 32 species of medusae (Table II). LDH and CS activities were measured in isolated swimming muscle of large medusae: *Pelagia colorata*, *Atolla wyvillei*, *Periphylla periphylla*, and *Solmissus incisa* (Table II). We could not detect octopine dehydrogenase in any species tested (whole-animal homogenates of *Pelagia colorata*, *Aurelia aurita*, an unidentified epipelagic hydromedusan, *Crossota rufobrunnea*, *Crossota alba*, *Haliscera conica*, *Haliscera bigelowi*, or isolated muscle of *P. colorata* and *P. periphylla*). We also could not detect either alanopine dehydrogenase or strombine dehydrogenase in any species tested (whole-animal homogenates of *C. rufobrunnea*, *C. alba*, *H. conica*, *and H. bigelowi* or isolated muscle of *P. periphylla*).

The highest CS activities were measured in the epiphytic medusa *Vallentinia adherens*. The highest LDH activities were measured in *P. periphylla*. Citrate synthase and LDH activities in *S. incisa* were lower than could be detected, but both these enzymes were measured at low levels in isolated swimming bell muscle. Citrate synthase could not be detected in whole-animal homogenates or in isolated coronal muscle of *A. wyvillei* and *A. vanhoeffeni*, although the coronate medusae of other genera had readily measurable CS activities. CS activity was higher than LDH activity in many of the species, although LDH activities were higher than CS activities in *A. citrea*, *H. maasi*, *Ptychogena lactea*, and the coronate scyphozoans *A. vanhoeffeni*, *A. wyvillei*, *P. periphylla*, and *Nausithoë rubra*. PK and MDH activities were usually higher with respect to their corresponding LDH and CS activities in the few species for which these enzymes were investigated; how-

Table I

Metabolic rates of medusae collected off California

Class Order Family Genus and species	Wet weight range (g)	T (°C)	Oxygen consumption (mean ± SE) (μmol O_2 g^{-1} h^{-1})	Number of specimens
Hydrozoa				
Leptomedusae				
Eirenidae				
Eirene mollis	0.1262–0.3896	15.0	0.783 ± 0.144	3
Anthomedusae				
Pandeidae				
Leukartiara octona	0.0629–0.3411	5.0	0.410 ± 0.091	3
	0.0322–0.9685	15.0	1.429 ± 0.223	5
Limnomedusae				
Olindiadidae				
Vallentinia adherens	0.0129–0.0536	15.0	1.932 ± 0.478	5
Trachymedusae				
Halicreatidae				
Botrynema brucei	1.3299	5.0	0.140	1
Haliscera bigelowi	0.191–1.1677	5.0	0.128 ± 0.030	5
Halitrephes maasi	13.070–27.386	5.0	0.046 ± 0.006	4
Rhopalonematidae				
Colobenema sericeum	2.4368–7.3620	5.0	0.091 ± 0.030	2
	5.858	10.0	0.199	1
Crossota alba	0.3180–0.8793	5.0	0.332 ± 0.128	3
Crossota rufobrunnea	0.062–1.08	5.0	0.154 ± 0.024	11
Crossota sp. A	0.1286–0.1445	5.0	0.168 ± 0.070	2
Pantachogon sp. A	0.3690–0.7157	5.0	0.259 ± 0.017	2
Tetrorchis erythrogaster	0.3987–0.4751	5.0	0.117	2
Vampyrocrossota childressi	0.2871–0.4127	5.0	0.140 ± 0.023	2
Narcomedusae				
Aeginidae				
Aegina citrea	0.3658–9.760	5.0	0.185 ± 0.037	11
Scyphozoa				
Coronatae				
Atollidae				
Atolla vanhoeffeni	0.6029	5.0	0.201	1
Atolla wyvillei	0.2192–17.22	5.0	0.134 ± 0.044	5
Nausithoidae				
Nausithoë rubra	0.5354–13.030	5.0	0.219 ± 0.048	2
Periphyllinidae				
Paraphyllina ransoni	0.1866–0.3453	5.0	0.333 ± 0.104	2
Periphyllidae				
Periphylla periphylla	2.7598–42.39	5.0	0.094 ± 0.017	8
	22.93	10.0	0.152	1

ever, PK was lower than LDH in the two coronates *A. wyvillei* and *P. periphylla*. We detected lactate in *P. periphylla* tentacle and coronal muscle at concentrations of 1.65 (SE = 0.45; $n = 6$) and 0.89 (SE = 0.28; $n = 6$) μmol g^{-1}, respectively. No lactate was detected in either velum tissue ($n = 4$) or tentacle tissue ($n = 4$) of *Aegina citrea*.

The common allometric scaling phenomenon of decreasing activity in larger individuals was observed in Krebs cycle enzyme activities (Fig. 2; Table III). LDH activities, on the other hand, increased with increasing wet weight (Fig. 3; Table III). The slopes of these regressions were different from zero at the 95% significance level. Nonsignificant negative scaling was observed for PK activities. Sufficient numbers of individuals of several species were analyzed to calculate species-specific scaling patterns, and the slopes of these regressions were usually not significantly different from zero over the size range studied. Significant allometric scaling relationships are presented in Table III.

Weight-specific CS activities were significantly correlated with weight-specific oxygen consumption rates at both 5 and 15°C (Fig. 4, F test for regression coefficient,

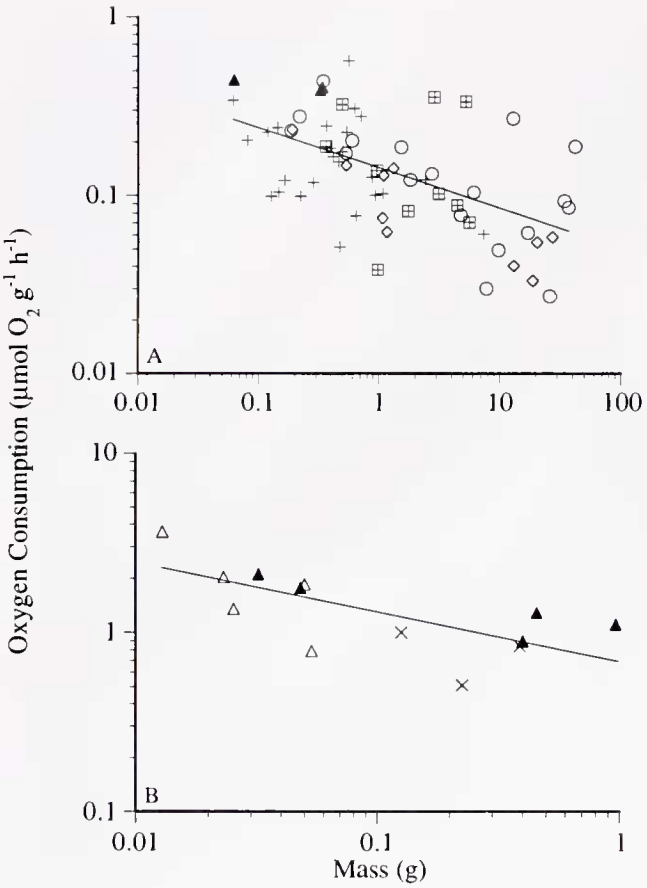

Figure 1. Oxygen consumption rates at 5°C (A) and 15°C (B) of California medusae as a function of their wet weight. The slope of the regression line for 5°C experiments is $y = 0.141\ x^{-0.22}$; $R = 0.45$. The slope of the regression line for 15°C experiments is $y = 0.712\ x^{-0.26}$; $R = 0.77$. Symbols for animals are as follows: Narcomedusae (⊞), Halicreatidae (^), Rhopalonematidae (+), Coronate scyphomedusae (○), *Vallentinia adherens* (△), Leptomedusae (×), *Leukartiara octona* (▲).

$P < 0.05$ for both regressions). Correlation coefficients were significant, $P < 0.05$ for both regressions, with $R = 0.31$ and 0.63 in the 5 and 15°C analyses, respectively.

Respiratory rate and enzyme activity in relation to depth of occurrence

No significant decline in metabolic rate or enzyme activity can be ascribed to minimum depth of occurrence in pelagic medusae (Figs. 5 and 6). The slopes of these regressions are not different from zero at the 95% significance level.

The slopes of the regressions describing the variation in metabolic rates and enzyme activities with depth are not statistically different from zero; however, they are significantly different from those for other groups that show significant declines in metabolic rates and enzyme activities with depth of occurrence. The pattern of change in medusan oxygen consumption rate with depth is significantly different from that observed for pelagic crustaceans (ANCOVA, $P < 0.02$; Fig. 5). The variation in CS activities with depth of occurrence in medusae (both with and without *V. adherens* data) is significantly different from the observed decrease in CS activity for pelagic fishes (ANCOVA, $P < 0.02$; Fig. 6A). The variation in LDH activities with depth in pelagic medusae is significantly different from that observed for pelagic fishes (ANCOVA, $P < 0.004$; Fig. 6B). Kendall's nonparametric test of rank correlation failed to show any significant correlation of mean medusan metabolic rate or enzyme activity with minimum depth of occurrence.

Discussion

Variability

Using an elaborate respirometer and a painstaking method of chemical analysis to determine oxygen and carbon dioxide content, Vernon (1895) was the first to measure the oxygen consumption rates of medusae. He observed considerable variability and, for the scyphozoan *Rhizostoma pulmo*, noted "distinct differences in the respiratory activity of different individual medusae" that could not be explained by size effects. Other investigators have also shown high variability in metabolic rate measurements of gelatinous animals (*e.g.*, Biggs, 1977; Larson, 1987b). One explanation may be that the nutritional status of the organism is reflected in metabolic rate measurements. Medusae undergo rapid periods of growth with high food concentration; furthermore, they "degrow" during periods of starvation and decrease in size to resemble a miniature adult (Hamner and Jenssen, 1974). Arai (1986) manipulated the nutritional status of the hydrozoan *Aequorea victoria* and observed higher metabolic rates in animals that had been starved for 3 days. She concluded that this was not due to behavioral changes and was unable to explain her findings. Other investigators have shown that nutritional status can be reflected in the enzyme activities of some organisms within days to weeks (Båmstedt, 1980; Clarke *et al.*, 1992; Clarke and Walsh, 1993; Lowery *et al.*, 1987; Roche-Mayzaud *et al.*, 1991). It is unknown how quickly enzyme activities in medusae are influenced by nutritional status.

Our investigation of enzymatic scaling in the demersal jellyfish *Polyorchis penicillatus* used individuals that were handled differently than other animals in this study, and the results of these experiments are less variable than results for the other species investigated. These *Polyorchis* had been kept in a planktonkreisel for up to 24 h with high concentrations of food. Perhaps the more uniform nutritional status of these individuals reduced the variability of their enzyme activity.

Table II

Enzyme activities of California medusae measured at 20°C

Class Family Genus and species	Minimum depth (m)	Wet weight range (g)	Enzymatic activity (mean ± SE, number of specimens)			MDH (units g^{-1})
			CS (units g^{-1})	LDH (units g^{-1})	PK (units g^{-1})	
Hydrozoa						
Polyorchidae						
Polyorchis penicillatus	10	0.079–14.690	0.238 ± 0.029, 11	0.172 ± 0.016, 11	0.216 ± 0.019, 3	0.939 ± 0.019, 3
Campanulariidae						
Phialidium lomae	10	0.010	0.118, 1	0.003, 1	n.a.	n.a.
Laodiceidae						
Ptychogena lactea	200	6.281	0.0004, 1	0.0230, 1	n.a.	n.a.
Eirenidae						
Eirene mollis	10	0.126–0.390	0.174 ± 0.056, 3	0.010 ± 0.005, 3	n.a.	n.a.
Pandeidae						
Leukartiara octona	10	0.008–0.054	0.402 ± 0.019, 3	0.020 ± 0.005, 3	n.a.	n.a.
Eutimidae						
Tima sp. A	100	0.2149	0.028, 1	0.004, 1	n.a.	n.a.
Olindiadidae						
Vallentinia adherens	10	0.008–0.054	3.563 ± 0.86, 6	0.057 ± 0.008, 6	n.a.	n.a.
Halicreatidae						
Botrynema brucei	600	1.299	0.002, 1	0.002, 1	n.a.	n.a.
Halicreas minimum	700	2.740–3.405	0.006, 1	n.d.	0.012, 1	0.005, 1
Haliscera bigelowi	800	0.191–1.641	n.d.	0.028 ± 0.009, 6	n.a.	n.a.
Haliscera conica	400	1.928	0.0007, 1	n.d.	n.a.	n.a.
Haliscera racovitzae	700	0.328–1.167	0.007,1	0.018 ± 0.007, 2	0.191 ± 0.013, 4	0.201 ± 0.047, 2
Halitrephes maasi	500	18.764–27.386	0.004 ± 0.001, 2	0.017 ± 0.005, 2	n.a.	n.a.
Rhopalonematidae						
Colobenema sericeum	300	2.437–9.319	0.124 ± 0.016, 3	0.031 ± 0.014	n.a.	n.a.
Crossota alba	100	0.296–0.879	0.179 ± 0.018, 6	0.008 ± 0.004, 6	n.a.	n.a.
Crossota rufobrunnea	500	0.062–1.080	0.147 ± 0.013, 13	0.011 ± 0.007, 13	0.145 ± 0.024, 4	0.578 ± 0.432, 4
Crossota sp. A	1100	0.1286–2.7281	0.038 ± 0.005, 4	0.006 ± 0.004, 3	n.a.	n.a.
Pantachogon sp. A	800	0.216–0.716	0.108 ± 0.012, 6	0.022 ± 0.004, 5	0.262 ± 0.053, 4	0.915 ± 0.131, 4
Tetrorchis erythrogaster	600	0.263–0.475	0.044 ± 0.019, 5	0.005 ± 0.001, 5	n.a.	n.a.
Tetrorchis sp. A	800	1.425	0.070,1	0.0007,1	n.a.	n.a.
Vampyrocrossota childressi	750	0.286–0.417	0.065 ± 0.011, 3	0.001 ± 0.0003, 3	n.a.	n.a.
Aeginidae						
Aegina citrea	800	0.366–9.760	0.043 ± 0.007, 11	0.085 ± 0.015, 11	0.285 ± 0.080, 4	0.624 ± 0.084, 4
Aegina sp. A	1000	6.602–17.440	0.003 ± 0.001, 2	0.001, 1	n.a.	n.a.
Cuninidae						
Solmissus incisa	1200	91.704	n.d.	n.d.	0.004, 1	0.009, 1
S. incisa (isolated swimming bell muscle)		93.5	0.007	0.003	n.a.	n.a.
Solmissus marshalli	10	5.015–17.292	0.006 ± 0.0, 2	0.028 ± 0.005, 2	n.a.	n.a.
Scyphozoa						
Atollidae						
Atolla vanhoeffeni	450	0.451–0.603	n.d.	0.318 ± 0.053, 3	n.a.	n.a.
Atolla wyvillei	500	0.219–71.050	n.d.	0.243 ± 0.055, 7	0.158 ± 0.008, 4	0.768 ± 0.208, 3
A. wyvillei (isolated coronal muscle)		71.05	n.d.	2.750	n.a.	n.a.
Nausithoidae						
Nausithoë rubra	1100	0.535–13.030	0.003 ± 0.001, 2	0.064 ± 0.028, 2	n.a.	n.a.
Periphyllinidae						
Paraphyllina ransoni	800	0.187–124.70	0.124 ± 0.044, 4	0.195 ± 0.088, 6	n.a.	n.a.
Periphyllidae						
Periphylla periphylla	650	2.204–36.05	0.017 ± 0.003, 5	1.711 ± 0.552, 5	1.112 ± 0.202, 3	0.669 ± 0.144, 2
P. periphylla (isolated coronal muscle)		20.0	0.215	5.659	n.a.	n.a.
Pelagiidae						
Pelagia colorata	10	3750.0–6800.0	0.225 ± 0.014, 2	0.015 ± 0.002, 2	n.a.	n.a.
P. colorata (isolated subumbrellar muscle)		6800.0	n.a.	5.08	n.a.	n.a.
Ulmaridae						
Aurelia aurita	10	98.4	0.019, 1	n.a.	n.a.	n.a.

CS: citrate synthase; LDH: lactate dehydrogenase; PK: pyruvate kinase; MDH: malate dehydrogenase; Units are micromoles substrate converted to product per minute. n.d.: not detected; n.a.: not assayed.

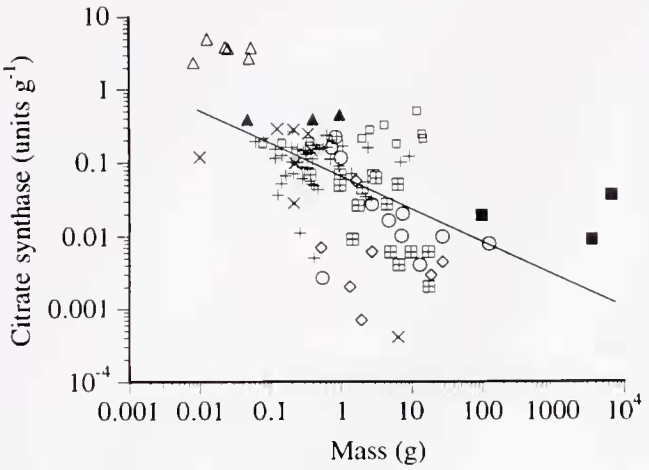

Figure 2. Citrate synthase activity as a function of wet weight for California medusae. The slope of the regression line is $y = 0.066x^{-0.44}$; $R = 0.67$. Symbols for medusae are given in Figure 1, and also include *Polyorchis penicillatus* (□) and other scyphomedusae (■).

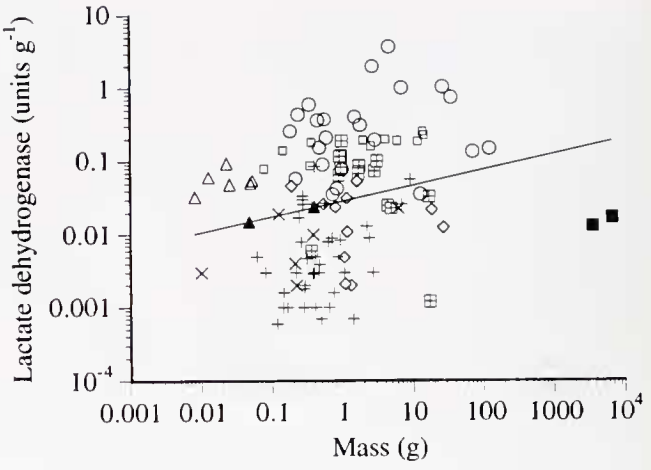

Figure 3. Lactate dehydrogenase activity as a function of wet weight for California medusae. Symbols for medusae are given in Figures 1 and 2. The slope of the regression line is $y = 0.027x^{0.22}$; $R = 0.08$.

This investigation included one species of "benthic" medusa: *Vallentinia adherens*. In contrast to the pelagic lifestyle of most medusae, *V. adherens* lives attached to kelp fronds and is exposed to much movement and water turbulence as it maintains itself near shore. We interpret the high CS activities in *V. adherens* as an indication of a metabolically robust animal that is adapted to life in such a high-energy environment. Thus, we believe that the interspecific variability of enzyme activities in the medusae investigated in this study indicates different physiological adaptations to their environments. For example, *Pelagia colorata* and *Periphylla periphylla* have LDH activities in swimming muscle comparable to those of the skeletal muscle of some of the deeper-living teleost fish, and most likely are active swimmers. Some of the species that have very low metabolic potentials are probably sit-and-wait predators maintaining their position in the water column with only periodic contractions of the swimming bell. Laterally flattened, or disk-shaped, medusae have lower CS activities than dorsoventrally elongated medusae, indicating that more hydrodynamic forms have higher metabolic potentials (for example, compare the more streamlined Rhopalonematidae with the Halicreatidae in Table II).

Enzymes

Some invertebrates use one or more amino acids as the terminal acceptor in glycolysis (Hochachka and Somero,

Table III

Allometric scaling relationships of enzymatic activities of pelagic medusae from California

		Enzymatic activity g^{-1} wet weight (y) as a function of total body wet weight (M), $y = aM^b$		
Group	Enzyme	a	b (±95% C.I., n)	$P<$
All medusae	CS	0.064	−0.43 (0.13, 102)	0.001
	LDH	0.027	0.22 (0.17, 112)	0.02
	MDH	0.434	−0.51 (0.39, 22)	0.02
All hydrozoans	CS	0.054	−0.37 (0.19, 82)	0.001
	LDH	0.015	0.45 (0.24, 81)	0.001
Rhopalonematidae	LDH	0.006	0.40 (0.37, 38)	0.04
Crossota alba	CS	0.236	0.47 (0.36, 6)	0.03
Polyorchis penicillatus	CS	0.213	0.10 (0.09*, 11)	0.08
	LDH	0.149	0.16 (0.09, 11)	0.01

Only regressions with slopes significantly different from zero are presented.
* 90% confidence interval.

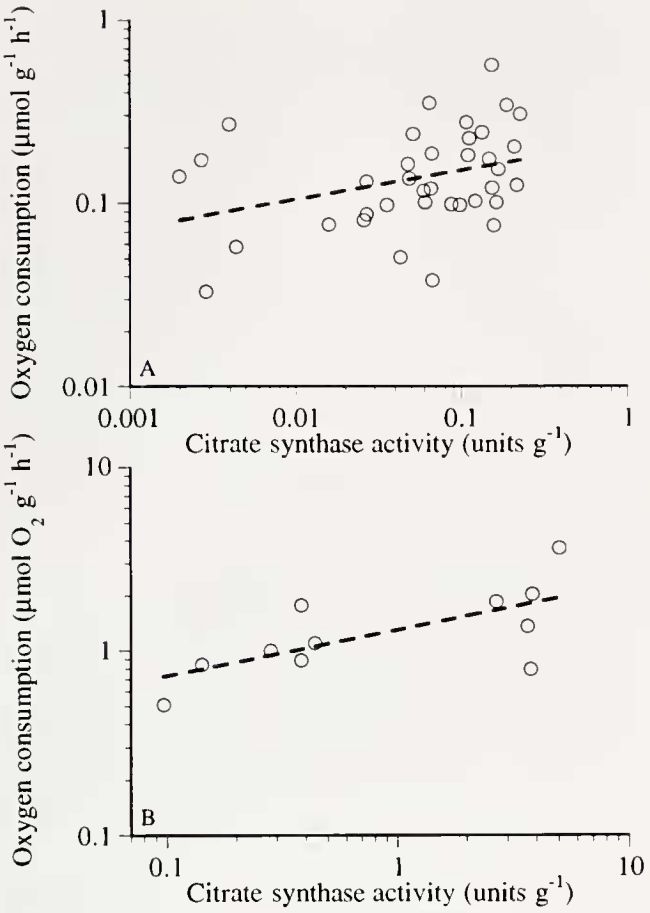

Figure 4. Relationships between citrate synthase activities and oxygen consumption rates measured at 5°C (A) and 15°C (B). The slope of the regression line for the 5°C data is $y = 0.216x^{0.16}$; $R = 0.31$. The slope of the regression line for the 15°C data is $y = 1.291x^{0.25}$; $R = 0.63$.

1984; Livingstone, 1991); these include some Cnidaria such as sea anemones (Walsh, 1981; Ellington; 1982). Although the biochemistry of glycolysis has been elaborated in several anthozoans (Livingstone, 1991; Shick, 1991), there are no previous reports on the enzyme biochemistry of scyphomedusae and hydromedusae. Our failure to detect octopine dehydrogenase, alanopine dehydrogenase, and strombine dehydrogenase in several species of scyphomedusae and hydromedusae suggests that these enzymes are either not present or not important in glycolysis in these cnidarians. The lactate levels we measured in *Periphylla periphylla* muscle (~1 μmol g^{-1}) are relatively high (*cf.* white muscle of rainbow trout at ~5 μmol g^{-1}; Milligan and Girard, 1993). Considering the low LDH activities of *Aegina citrea* compared with *P. periphylla* (Table II), it is not surprising that we were unable to detect lactate in *A. citrea*—the quantities of lactate in our *P. periphylla* samples were already in the lower range of accurate detectability. It is possible that some of the other medusae that we did not assay for -opine dehydrogenases do in fact have significant -opineDH activity. Furthermore, we have not assayed for the enzymes of other known anaerobic pathways or their endproducts (*e.g.*, succinate, propionate), and our limited data on cytosolic MDH do not allow us to assess its role in medusan anaerobic metabolism. Future studies on the evolution of glycolytic pathways in Cnidaria clearly should include specimens from the Scyphozoa, Hydrozoa, and Cubozoa.

The metabolic poise of most of the medusae studied seems to be aerobic, as CS activities were higher than corresponding LDH activities. The most notable exceptions are the meso- and bathypelagic coronate medusae. Several explanations are possible for the evolution of higher glycolytic potentials in these medusae. Coronates are apparently active predators (Larson, 1979) and may need an anaerobic energy supply during periods of active swimming in search of prey. Mills and Vogt (1984) found that epipelagic hydromedusae do not use ionic regulation as a buoyancy aid in vertical migrations. They proposed that these medusae must rely solely on swimming for diel vertical migrations. Although we did not find that the epipelagic hydromedusae in our study were anaerobically poised, they are likely using LDH for sustained bouts of swimming. Coronate medusae are also vertical migrators (Alvariño, 1967), and they may need an anaerobic energy supply if they are constantly swimming during periods of ascent and descent through the water column. Furthermore, as these organisms move through the water column, they spend considerable time in water of low oxygen concentration, the oxygen minimum layer (Wyrtki, 1962,

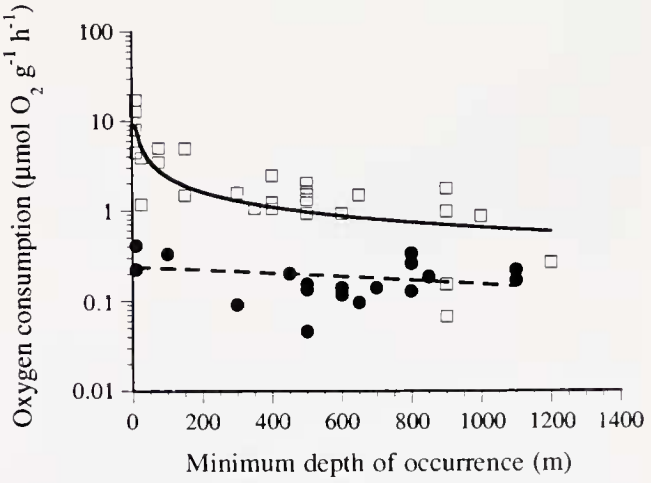

Figure 5. Metabolic rates of California medusae (●) as a function of minimum depth of occurrence (Table I) compared to pelagic crustacean data (□) from the same region. The slope of the regression line for medusan data is not significantly different from zero. The slope of the regression line for the crustacean data is $y = 32.819x^{-0.57}$; $R = 0.81$ (Childress, 1975). Results of ANCOVA show that the regressions of the two groups are significantly different from one another, $P < 0.02$.

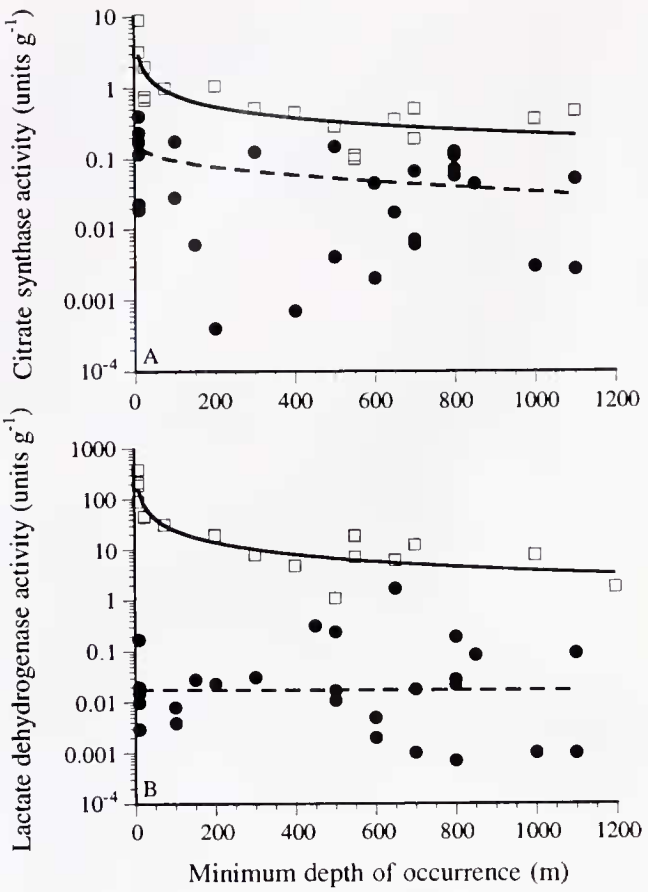

Figure 6. (A) Citrate synthase activities of California medusae (●) as a function of minimum depth of occurrence (Table II) compared to pelagic fish data (□) from the same region. The slope of the regression line for medusan data is not significantly different from zero. The slope of the regression line for the fish data is $y = 10.355x^{-0.56}$; $R = 0.77$ (Childress and Somero, 1979; Wells and Childress, unpub.). Results of ANCOVA show that the regressions of the two groups are significantly different from one another, $P < 0.02$. (B) Lactate dehydrogenase activities of California medusae (●) as a function of minimum depth of occurrence (Table II) compared to pelagic fish data (□) from the same region. The slope of the regression line for medusan data is not significantly different from zero. The slope of the regression line for the fish data is $y = 1000.5x^{-0.81}$; $R = 0.84$ (Childress and Somero, 1979). Results of ANCOVA show that the regressions of the two groups are significantly different from one another, $P < 0.01$.

1967). If they cannot supply their metabolic needs aerobically while in the oxygen minimum layer, they would need an anaerobic energy source for survival.

Comparison of our previous results on CS activity and oxygen consumption rate correlations in pelagic worms (Thuesen and Childress, 1993a, b) and fishes (Childress and Somero, 1979) with the present data on medusae shows that medusae have lower rates of oxygen consumption in relation to CS activities than do the other groups. That is, medusae have more CS relative to their oxygen consumption rates than do polychaetes, nemerteans, chaetognaths, and fishes. King and Packard (1975) found that the ratio of ETS activity to oxygen consumption was significantly higher in epipelagic hydrozoans than in the "non-medusoid zooplankton" they studied. Furthermore, the relation between oxygen consumption and CS activity in the medusae in the present study was not directly proportional, because increasing increments in CS are correlated with proportionately much smaller increases in oxygen consumption rates. The increase in CS activity is directly proportional to the increase in oxygen consumption rate in pelagic polychaetes and fishes (Thuesen and Childress, 1993b; Childress and Somero, 1979). Our data also show the following relationship in correlation coefficients: R (0.94) in pelagic polychaetes and nemerteans > R (0.58) in chaetognaths > R (0.31) in medusae. We propose that in animals such as medusae, which lack mechanisms for transport of oxygen within their bodies, the diffusion of oxygen may limit the effectiveness of oxygen supply to mitochondria while the inherent properties of the mitochondria and associated enzymes may remain the same as in other groups. Therefore, the mitochondrial aerobic metabolism realized *in vivo* would be limited by the supply of oxygen in these animals. The suggestion that the mitochondrial metabolism is limited by oxygen diffusion to the mitochondria is supported by our preliminary findings that these medusae generally show a dependent pattern of metabolism when exposed to lower oxygen concentrations. In such a situation, the synthesis of "excess" metabolic enzymes or mitochondria may be an important mechanism to maximize the use of the available oxygen.

The existence of oxygen-limited aerobic enzymes would account for the high ratios of CS or ETS activities to oxygen consumption rates and also partially explain the low correlation we found between medusan enzyme activities and oxygen consumption rates. A similar situation may exist in sea anemones (Shick, 1991). High-shore individuals of the intertidal anemone *Anthopleura elegantissima* have higher cytochrome *c* oxidase activities and greater numbers of mitochondria than low-shore individuals; however, the mass-specific oxygen consumption rates are lower in the high-shore individuals. Therefore, although enzyme activities measured at V_{max} may correlate well with oxygen consumption rates in animals such as crustaceans and fishes, which have evolved efficient oxygen uptake and transport systems, this method is evidently not a good one for predicting the metabolic rates of some gelatinous organisms.

This interpretation of our results does not agree with the physiological hypothesis of symmorphosis, which states that the structural designs of organisms are quantitatively matched to functional demands (Weibel *et al.*, 1991). The symmorphosis hypothesis predicts that the quantity and efficiency of aerobic enzymes should be

matched with oxygen supply. Although enzyme activities and oxygen supply may be in balance in mammals, which have well-developed circulatory systems, oxygen diffusion and enzyme activities may not be in balance in medusae, which rely on direct diffusion from the environment to supply mitochondria with oxygen, if mitochondria at the periphery of diffusion distance are oxygen-limited.

Furthermore, different body tissues have different metabolic potentials and oxygen diffusion characteristics, and the contribution of muscle, gonads, mesoglea, *etc.*, to whole-organism respiration will be different, depending on the proportion of these tissues in each individual. In *Aurelia aurita*, different tissues can grow and degrow at different rates depending on animal size and nutritional state (Hamner and Jenssen, 1974). This implies that animals of identical body mass could have different proportions of metabolically active tissue, and could explain some of the variation observed in weight-specific metabolic relationships. For example, if mesoglea, a relatively metabolically inactive tissue, degrows first (de Beer and Huxley, 1924), the result would be an increase in mass-specific oxygen consumption with starvation. This could explain some of the variation observed in weight-specific metabolic relationships, as well as the observations, discussed earlier, made by Arai (1986) on the effects of starvation on the hydrozoan *Aequorea victoria*.

Scaling

Previous observations on the intraspecific metabolic scaling of gelatinous animals have found small or non-significant effects of size on oxygen consumption rate (*e.g.*, Kremer *et al.*, 1986; Larson, 1987b; Vernon, 1895). We have observed very little species-specific scaling, possibly because of variation in nutritional condition and tissue growth, as discussed above. However, it would appear that medusae do exhibit an overall trend toward lower specific metabolic rates in larger animals.

Our results also indicate that glycolytic potentials are elevated in larger medusae. This could indicate an increase in muscle mass relative to body mass or an increase in LDH activity per gram of muscle tissue. One study on the coastal scyphomedusa *Stomolophus meleagris* from the Gulf of Mexico has shown that in this species, unlike most other aquatic animals, transport costs do not continue to decline with size in larger animals, although they do decline with increasing body mass in smaller specimens (Larson, 1987a). This could result in larger medusae having elevated LDH activities to maintain their swimming performance. Another explanation may be that higher LDH activities in larger medusae are a consequence of greater oxygen diffusion distances, as discussed above for CS activities. Some fish show positive scaling of glycolytic enzymes, and this has been interpreted as an adaptation for size-independent acceleration used during predator-prey interactions (Childress and Somero, 1990; Somero and Childress, 1980, 1990). We do not think that this is the cause of the scaling pattern we observed, because medusae are poor accelerators. Larson (1987a) found little acceleration ability in *S. meleagris* and observed negative scaling of pulsation rate ($b = -0.12$). He concluded that medusae are cost-efficient swimmers because their proportionally small amounts of metabolically active tissue result in low energy usage. The general trends of negative scaling of aerobic metabolism and positive scaling of glycolytic potential with size may be common physiological phenomena in medusae.

Minimum depth of occurrence

No significant change in metabolic rates or metabolic potentials, as determined by enzymatic activities of the medusae, can be attributed to depth of occurrence. These results are in contrast to the patterns of metabolic rates seen in fishes and crustaceans, and they support the visual interactions hypothesis, because nonvisual animals would not be expected to show a metabolic decline with depth *per se* if the driving selective force behind the adaptation was the light regime of the environment. These results, along with the results of a previous study on chaetognaths (Thuesen and Childress, 1993a), confirm the differences between visually orienting and nonvisually orienting pelagic animals in their patterns of metabolic rate with increasing habitat depth.

According to the visual interactions hypothesis, reduced reliance on vision decreases selection for locomotory abilities; the locomotory ability of the bathypelagic mysid *Gnathophausia ingens* has been shown to be reduced compared to those of shallower-living crustaceans (Cowles and Childress, 1988). We predict that a comparison of morphologically similar medusae would not show lower locomotory abilities in bathypelagic species; many deeper-living species are in fact very robust. Investigations of benthic organisms do not show depth-related metabolic declines other than those that can be explained by the effects of temperature and size (Childress *et al.*, 1990a; Shirayama, 1992). These findings are in agreement with the visual interactions hypothesis, because little change in behavior with depth would be expected in animals that use the bottom substrate for concealment.

The other hypothesis that has been proposed to account for the widely observed decline in metabolic rates of pelagic animals—the food limitation hypothesis—suggests that animals living in a relatively food-poor environment have evolved lower metabolic rates as a way of conserving energy (Childress, 1971; Smith and Hessler, 1974). If food availability were a contributing factor in the evolution of metabolic rates, one could

expect that the animals in regions of low productivity would have evolved lower metabolic rates than similar animals in highly productive environments. Contrary to this prediction, several studies have found pelagic crustaceans living in regions of different food availability to have similar metabolic rates (see review in Childress and Thuesen, 1992). Food limitation may be less of a problem for deep-living medusae, because potential prey organisms are so energy rich in comparison to medusan predators (Thuesen and Childress, unpub. data).

Another obvious variable with increasing depth is the increase in hydrostatic pressure. In a separate study, we tested the effects of pressure on the metabolic rates of *Aegina citrea, Crossota rufobrunnea,* three species of Chaetognatha, and a mesopelagic polychaete worm, *Poeobius meseres* (Childress and Thuesen, 1993). We observed no significant differences in metabolic rates measured at 1 atm and 101 atm ($\approx$1000 m) in any of these animals. Most previous studies have also found that the metabolic rates of mesopelagic and bathypelagic organisms show little change due to hydrostatic pressure when measured within the range of their normal habitat pressures (Belman, 1978; Quetin and Childress, 1976; Smith and Teal, 1973; Teal and Carey, 1967; Torres and Childress, 1983).

The high values of Q_{10} for oxygen consumption rate that we measured could have been influenced by increased activity at higher temperature. Although Mangum *et al.* (1972) observed similarly high Q_{10} values of oxygen consumption rates and bell pulsation rates for nonacclimated polyps of *Aurelia aurita* and *Chrysaora quinquecirrha,* they observed lower values of Q_{10} in medusae of *Cyanea capillata* acclimated for 3 days at each temperature. Vertically migrating medusae such *Colobenema sericeum* and *Periphylla periphylla* (estimated Q_{10} values of 4.8 and 2.6, respectively, in our study) could be expected to experience rapid changes in temperature on a regular basis, and our Q_{10} data indicate that they are not insensitive to such temperature changes or that their activity is stimulated by increased temperature. Therefore, the only physical parameters expected to contribute to differences in the metabolic rates of nonvisually orienting pelagic animals are those due to differences in water temperatures and oxygen concentrations.

Although deep-living gelatinous organisms are able to exploit the energy resources of lipid-rich vertically migrating crustaceans and have evolved life histories and energy-use strategies in response, their metabolic rates reflect no obvious selective pressure related to depth of occurrence. The absence of a depth-related decline in medusan metabolism means that the metabolic rates of deep-sea medusae approach those of deep-sea fishes and crustaceans, and therefore, medusae play a more important role than previously expected in the carbon flux of mesopelagic and bathypelagic environments.

Acknowledgments

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